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HABITAT SELECTION BY SPOTTED OWLS DURING NATAL DISPERSAL IN WESTERN OREGON

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Abstract: The probability of successful natal dispersal may influence the viability of northern spotted owl (*Strix occidentalis caurina*) populations within fragmented forests. We tested 6 null hypotheses examining the relations between habitat selection, forest fragmentation, and the probability of mortality for juvenile northern spotted owls during natal dispersal in western Oregon, 1982–85. Older forest (old-growth and mature stands) was the vegetation type used most frequently during transience (35.3%) and colonization (61.2%), and spotted owls selected closed-canopy forests over open-canopy forests during both phases of dispersal (P < 0.05). The hypotheses that spotted owl habitat selection was independent of forest fragmentation were not rejected for either transient ($P = 0.51$) or colonization ($P = 0.43$) dispersal. Likewise, net dispersal distance was independent of forest fragmentation ($P = 0.92$). Use of open sapling stands during transient dispersal decreased the probability of mortality (Wald test = 2.21, $P = 0.03$), whereas use of clearcuts during colonization dispersal increased the probability of mortality (Wald test = 1.95, $P = 0.03$). Net dispersal distance did not affect the probability of mortality ($P = 0.67$), yet a negative relation existed between dispersal distance and the amount of clearcut used during transient dispersal ($P < 0.005$). These results provide additional evidence of the selection of older forests by spotted owls and how their natal dispersal may be affected by harvesting such forests; particularly, that use of clearcuts may decrease the probability of successful natal dispersal.

Key words: dispersal, forest fragmentation, habitat selection, mortality, natal dispersal, Oregon, spotted owls, *Strix occidentalis caurina*, survival.

Estimates of habitat-specific demographic parameters are required to develop effective species-specific management and conservation strategies (Van Horne 1983, Murphy and Noon 1991, Pulliam et al. 1992, Soulé and Kohm 1989). The understanding of dispersal is severely limited when compared to survival and reproduction (Taylor 1990), and may preclude realistic efforts to manage for faunal movement across landscapes (Harrison 1992). The importance of dispersal in sustaining viable populations also is receiving increased attention in wildlife conservation (Kareiva 1990, Newton 1991*a*, Pulliam and Danielson 1991), especially within fragmented landscapes (Temple 1989, Weins 1990, Rolstad 1991).

The northern spotted owl is closely associated

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with older-aged forests, and younger forests that contain residual older forest components (i.e., large trees, snags and downed woody material), in the Pacific Northwest and the species' decline is believed to be due to the loss and fragmentation of such forests (Thomas et al. 1990). Determining dispersal attributes and factors that influence survival during dispersal will become increasingly important with increased fragmentation (Noon and Biles 1990). If owls select older forests during dispersal, the loss and fragmentation of those forests could reduce the probability of juveniles locating areas to establish a breeding territory. Successful dispersal would decrease because juvenile owls would be required to disperse greater distances over potentially unsuitable habitat, during a period of high mortality (Gutiérrez et al. 1985, Miller and Meslow 1985). Thus, as older forests become more scarce and more patchy in distribution, population viability may be reduced. Population modeling suggests spotted owl viability is sensitive to dispersal dynamics (Doak 1989, Lande 1991, Lamberson et al. 1992, Lamberson et al. 1994); thus, dispersal has been an important

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component in the conservation strategies developed for spotted owls (Thomas et al. 1990, Harrison et al. 1993, U.S. Dep. Agric. et al. 1993).

To better understand the role of dispersal in populations of spotted owls, we tested 6 null hypotheses concerning the relation between habitat selection, forest fragmentation, probability of mortality, and dispersal distance: (1) dispersing juvenile owls select older-aged forests over younger-aged forests, (2) dispersing juvenile owls select equally between less fragmented forests and more fragmented forests, (3) the probability of mortality of dispersing juvenile owls in younger-aged forests is equal to that in older-aged forests, (4) the probability of mortality of dispersing juvenile owls in more fragmented forests is equal to that in less fragmented forests, (5) the probability of mortality of juvenile owls is independent of their natal dispersal distance, and (6) natal dispersal distance is independent of the amount of forest fragmentation.

STUDY AREAS

Based on the location of nesting adult spotted owls (Miller 1989), we selected 7 areas in western Oregon to examine natal dispersal during 1982–85 (Fig. 1). Six areas were within the Western Hemlock Zone, the most extensive vegetation zone in western Oregon and the most important for timber production (Munger 1930, Franklin and Dyrness 1973). Subclimax Douglas-fir (*Psuedotsuga menziesii*) dominated this zone, with western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) the 2 other major tree species. A mild, maritime climate of relatively dry summers and wet winters characterized the Western Hemlock Zone, with winter precipitation falling as rain at lower elevations, especially in the Coast ranges, and as snow at higher Cascade elevations (Franklin and Dyrness 1973). These areas occurred on the Willamette National Forest (NF), Salem District BLM, Eugene District BLM, and the northern portion of Roseburg District BLM. The seventh area was in the southern portion of the Roseburg District BLM, a transition area between the Western Hemlock and Mixed Conifer zones (Franklin and Dyrness 1973). The Mixed Conifer Zone was generally hotter and drier during the summer months than the Western Hemlock Zone, and in addition to Douglas-fir, the predominate tree species were sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), incense cedar (*Libocedrus decurrens*), and grand fir (*Abies grandis*). Clearcutting was the predominate logging method in all study areas.

Once juvenile owls dispersed from their natal forested regions in the Western Hemlock Zone, they used the 3 interior valleys of western Oregon: the Willamette, Umpqua, and Rogue. The vegetation within these valleys was a mosaic of grassland, oak woodland, conifer forest, evergreen shrub, and riparian communities (Franklin and Dyrness 1973). Urban, suburban, and agricultural areas also were present within the interior valleys.

METHODS

Telemetry

We visually relocated juvenile owls for 3–4 weeks after fledging (late May through mid-Jun) until they gained sufficient weight (at or near ad wt) and could fly to elevated perches before we equipped them with radiotransmitters. Using either a noose pole or long-handled dip net (Forsman 1983), we captured and then fitted owls with backpack radiotransmitter packages consisting of AVM SM-1 modules (AVM Instrument Co., Livermore, Calif.) and 5-mm teflon tubing for straps. The total weight of the transmitter packages was ≤23 g (3–4% body wt). We used a Telonics TR-2 receiver and hand-held, 2-element, Yagi antenna (Telonics, Mesa, Ariz.) to relocate owls. When visual confirmation was not possible, we estimated owl locations by tri-
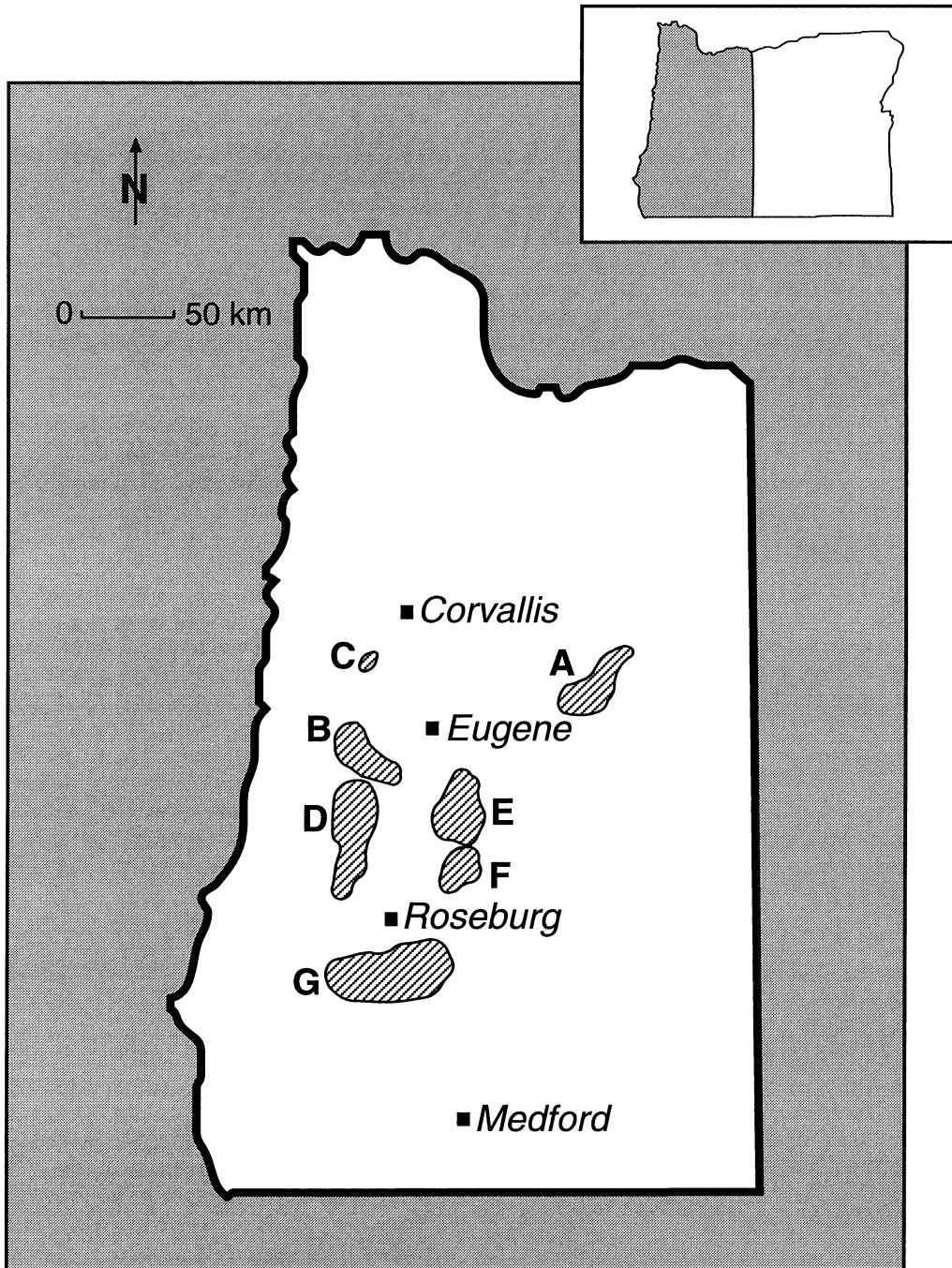
Fig. 1.   Study area locations for habitat selection of spotted owls during natal dispersal in western Oregon, 1982–85: (A) H. J. Andrews Experimental Forest vicinity—Cascades; (B) Eugene District BLM lands—Coast ranges; (C) Salem District BLM lands—Coast ranges; (D) Roseburg District BLM lands—Coast ranges; (E) Eugene District BLM lands—Cascades; (F) Roseburg District BLM lands—Cascades; (G) Roseburg District BLM lands—transition area.

angulation using at least 3 bearings. After the initiation of dispersal, we monitored owls daily if time and weather permitted. If dispersing owls could not be relocated by ground crews, we used aircraft equipped with 2, 2-element, Yagi antennas to find the birds.

We considered natal dispersal to begin when an owl left its natal area (the area where it spent

the summer) and to continue until the initiation of breeding (Greenwood 1980). Hence, juvenile spotted owls generally continue their natal dispersal until at least 2 years old (their third spring/summer), but more commonly 3 years old (Miller 1989, Wagner and Meslow, unpubl. data). In addition, we considered the dispersal process as 2 separate phases: transience, a period of extensive movement from 1 area to another, and colonization, the period when an animal attempts to become established in a new area (Johnson and Gaines 1985, Small et al. 1993). The initiation of transient dispersal was clearly detectable, because the movement of juvenile owls away from their natal areas was distinct and rapid. Cessation of transience, and thus the initiation of colonization dispersal, also was easy to detect because most owls began to roost in relatively discrete areas for the rest of their first winter. Specifically, we considered groups of ≥5 consecutive locations in an area ≤2.4-km radius to represent colonization areas. A 2.4-km radius represented an average home range size for spotted owls in western Oregon (Forsman et al. 1984). Owl locations within such areas were classified as colonization dispersal, whereas all other owl locations were classified as transient dispersal.

Habitat Classification

We recognized 5 vegetation types (Hall et al. 1985) in the habitat selection analysis: (1) older forest (old-growth and mature stands), characterized by stands with an average diameter at breast height (dbh) >53.3 cm and usually <100% crown canopy closure, at least 2 height classes of trees, decay in living trees, snags, and downed woody material; (2) closed sapling-pole-sawtimber stands, characterized by trees of 2.5–53.3-cm dbh and crown canopy >60%; (3) open sapling-pole stands, characterized by stands >2.5-cm dbh and crown canopy <60% (saplings were 2.5–10.2-cm dbh, poles 10.2–22.9-cm dbh); (4) clearcuts (i.e., grass/shrub) characterized by trees <2.5-cm dbh and <40% crown canopy; and (5) "other", which included reservoirs, rock outcrops, pastures, and towns.

We delineated these vegetation types by interpreting aerial photographs and orthophotoquads from each NF or BLM district forest stand information. Satellite imagery (Landsat) information was available for some parts of the Cascade study areas, and we used it to assist interpretation.

Habitat Use and Availability

We used a circular sampling grid of 1.6-km radius (ca 10 km^2) to estimate habitat use and availability; 1.6 km represents the mean daily straight-line dispersal distance of juvenile owls during transient dispersal (Miller 1989). The average distance between successive sampling grids was about 6.6 km (4.1 × 1.6 = 6.6; 4.1 = $\bar{x}$ no. days between successive locations), resulting in non-overlapping samples. The grid center was placed on each estimated owl location (see below), with the grid being divided into 112 0.3- × 0.3-km cells. Each cell represented the approximate size (9 ha/22 acres) of an average forest harvest unit. To randomize grid sampling with respect to any landscape patterns, the grid was rotated randomly 0–45 degrees for each location and random point. We then used 50 uniformly spaced grid cells, out of the 112 cells available in the overall grid, and 50 uniformly spaced cell intersections to estimate habitat homogeneity and percentage of each vegetation type, respectively, within the 1.6-km circular grid landscape for each location.

We estimated habitat use for each transient and colonization owl location to be the percentage of each vegetation type at the 50 selected points (cell intersections) within the sample grid. Habitat homogeneity for each location was estimated by the proportion of the 50 selected cells in the sampling grid that contained 100% of 1 of the 2 closed-canopy forest types (older forest or closed sapling pole). We then indexed forest fragmentation for each 1.6-km radius circle sampling grid by combining the homogeneity score with the proportion of older forest, (1.0 − [homogeneity score + proportion older forest]/2), resulting in a fragmentation index value between 0.0 and 1.0. Thus, low fragmentation indices were obtained for grids containing relatively large contiguous stands of closed canopy forests, whereas grids composed primarily of open sapling pole stands and/or fragmented by recent timber harvesting received higher fragmentation indices.

For each owl location recorded during transient dispersal, we selected 2 1.6-km radius sampling grids to estimate habitat availability. The location of these grids was based on the bearing and distance between 2 consecutive owl locations, designated O_1 and O_2. Specifically, 2 vectors were established, each originated at O_1 and set at 45 degree angles on either side of the dispersal path between O_1 and O_2; the length of

the vectors equaled the distance between O_1 and O_2 (Miller 1989). We then centered the availability sampling grids at the end of the 2 vectors, and measured the habitat characteristics (% of each vegetation type and fragmentation) as outlined above.

We selected 4 sampling grids to estimate habitat availability for each colonization area; an individual juvenile could have several colonization areas. We determined the location of these grids by first creating a polygon that circumscribed the locations within each colonization area, then fixed 4 vectors in the 4 cardinal directions originating from the center of the polygon. A vector's length equaled the greater of (1) twice the distance from the polygon center to the edge of the polygon along each vector, or (2) 1.6 km from the edge of the polygon. We then calculated mean habitat characteristics from the 4 availability samples, and compared this mean to the mean from the locations within the colonization area. Sampling methodology for habitat use and availability was described in greater detail by Miller (1989).

Statistical Analyses

We chose the Friedman test (Conover 1980) to examine selection among the 5 habitats by dispersing juvenile owls. This method gives equal weight to all animals, regardless of the number of observations on each, and tests the hypothesis that ranks of differences between use and availability for each animal are the same for all habitats (Alldredge and Ratti 1986, 1992). If this hypothesis was rejected, we used the conservative Tukey's multiple comparison test (Day and Quinn 1989) to determine how owls selected among the 5 habitats. To compare selection strategies for each habitat among individual owls we plotted individual selection variability (Thomas and Taylor 1990). We grouped fragmentation indices into 3 levels: low, ≥ 0.0 and < 0.4; medium, ≥ 0.4 and < 0.7; and high, ≥ 0.7 and < 1.0. We then used the Friedman test to determine if there was selection among the 3 levels of fragmentation.

To determine if the forest structure used by juvenile owls during dispersal affected their probability of mortality, we performed regression analyses using the nonparametric Cox proportional hazard model (Cox 1972, Johnson 1994:408). The number of days an owl survived after it began transient dispersal, including the number of days in colonization, was entered as the dependent variable, and interpreted as an index to the probability of mortality. Only known mortalities were treated as "failures", with unknown losses (e.g., signal loss) designated as censored. Due to the small number of mortalities recorded, we assumed survival was equal among years. The percentage of each vegetation type and the fragmentation index during both transience and colonization dispersal were entered as independent variables (covariates). We also tested whether these covariates influenced dispersal distance by using the net dispersal distance as the dependent variable. Only the data from owls that survived transient dispersal during their first autumn of life were used for this test, with net distance defined as the straight-line distance between the natal area and the location of death or the location on 31 May of the following year; that date represented the general 1-year anniversary from fledging. Final regression model selection was based on results from entering each covariate individually, and both forward and backward stepwise procedures. The Wald test was used to determine which covariates significantly influenced the dependent variables.

RESULTS
Habitat Selection

Older forest was the most frequently used habitat during both transient and colonization dispersal; yet, colonization areas occurred in older forests at nearly double their availability (61 vs. 33%) whereas the difference during transient dispersal was small (35 vs. 31%; Table 1). Habitat selection by individual owls also indicated disparate selection patterns between the 2 periods of dispersal (Fig. 2). During colonization, differences between use and availability were consistently positive and relatively greater for closed-canopy forests than the negative values observed for open-canopy forests; most differences were relatively small for all habitats during transience.

Juvenile owls selected among the 5 habitats in a similar manner during both periods of dispersal, based on the mean ranks of differences between habitat use and availability: older forest, closed sapling, "other", open sapling, and clearcut (descending order) (transience: $T_2 = 2.30$; 4, 80 df; $P < 0.06$; colonization: $T_2 = 15.32$;

Table 1. Habitat use and availability for juvenile spotted owls during transient dispersal and at roosting areas, western Oregon, 1982–85.

Habitat	Transient dispersal[a]				Colonization dispersal[b]			
	Use		Availability		Use		Availability	
	$\bar{x}$%	SE	$\bar{x}$%	SE	$\bar{x}$%	SE	$\bar{x}$%	SE
Old-growth	35.3	16.1	31.1	16.2	61.2	33.0	33.3	18.1
Closed sapling	23.5	10.8	25.8	11.7	28.7	28.6	22.4	12.7
Open sapling	18.2	10.2	18.8	8.1	8.2	11.2	19.1	10.5
Clearcut	17.1	9.5	17.9	10.7	1.2	2.1	17.1	11.1
Other[c]	5.9	8.2	6.5	8.7	1.1	2.0	7.9	12.0

[a] $n = 21$; ranks of differences between use and availability significant at $P < 0.07$.
[b] $n = 18$; ranks of differences between use and availability significant at $P < 0.001$.
[c] Pastures, reservoirs, towns.

4, 68 df; $P < 0.001$). The results from the subsequent Tukey multiple comparison tests suggested evidence of selection ($P < 0.05$) for 2 groups of habitats during transient dispersal. Owls selected older forests, closed saplings, and "other" habitats disproportionately more or equal to their availability, whereas open sapling and clearcuts were used proportionately less than expected based on availability (Fig. 2). During colonization, there was evidence of selection ($P < 0.05$) for 3 groups of habitats; older forests were selected disproportionately more relative to their availability, closed sapling and "other" were selected slightly less than expected, and open sapling and clearcut were selected less relative to all other habitats.

Juvenile owls did not exhibit selection among the 3 levels (low, medium, high) of fragmentation during either transience ($T_2 = 0.72$; 2, 20 df; $P = 0.51$; Fig. 3) or colonization ($T_2 = 0.94$; 2, 15 df; $P = 0.43$; Fig. 4). Likewise, net dispersal distance was independent of the amount of fragmentation (Wald test = 0.10, $P = 0.92$). Net dispersal distance decreased with an increased use of clearcuts during transience (Wald test = 2.42; $P = 0.005$; Fig. 5); the use of all other habitats did not significantly ($P > 0.05$) affect dispersal distance.

Mortality

Only 2 habitat parameters significantly ($P = 0.03$) affected the probability of mortality during dispersal; an increased use of open sapling stands during transience decreased the probability of mortality (Wald test = 2.21; Fig. 6), whereas an increased use of clearcuts during colonization increased the probability of mortality (Wald test = 1.95; Fig. 7). Net dispersal distance did not affect the probability of mor-
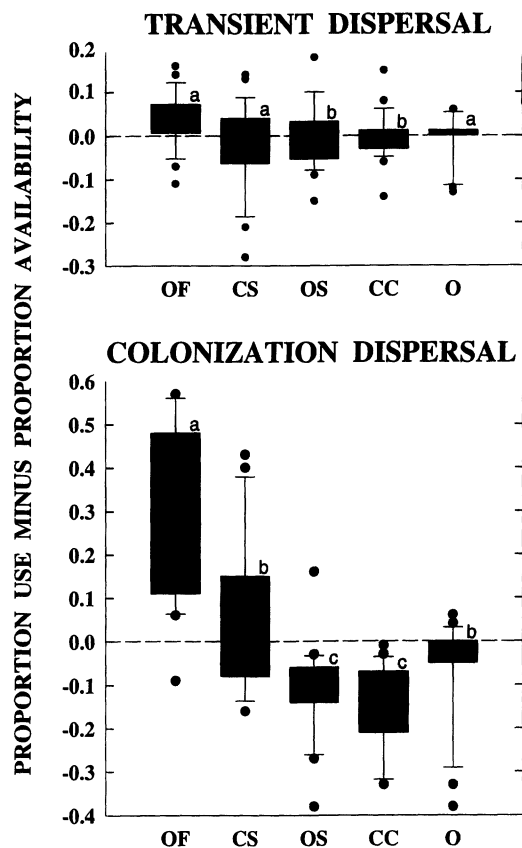
Fig. 2. Habitat selection variability among individual juvenile spotted owls during transient dispersal ($n = 21$) and colonization ($n = 18$), western Oregon, 1982–85. Boxes indicate the 25–75th percentile range and contain the median line, whereas capped bars represent the 10th and 90th percentile values; closed dots represent points outside these values. Lower case letters designate groups of habitats which owls selected in a similar manner relative to availability. OF = older forest; CS = closed sapling; OS = open sapling; CC = clearcut; O = "other" (see text).
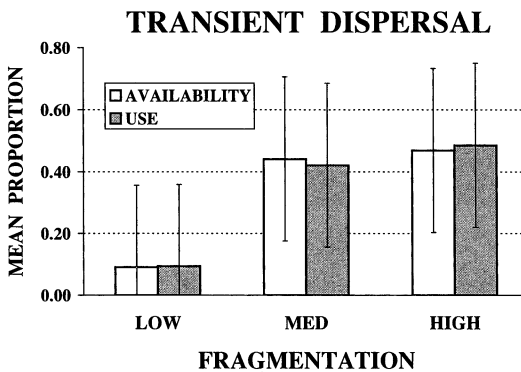
Fig. 3.   Mean percent use and availability, based on the extent of fragmentation, during transient dispersal of juvenile spotted owls (*n* = 21), western Oregon, 1982–85. Error bars represent standard error.
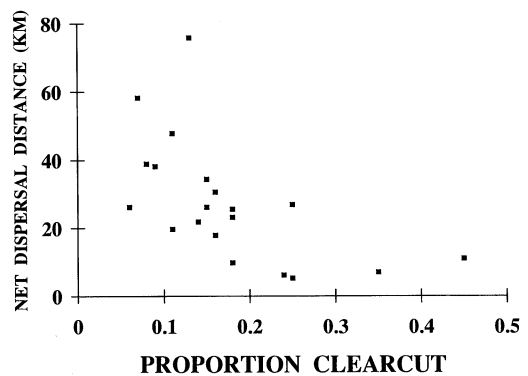

Fig. 5.   Mean percent clearcut used during transient dispersal of juvenile spotted owls (*n* = 20) in western Oregon, 1982–85, compared to their net dispersal distance.

tality ($t = 0.45$, $P = 0.67$), based on a comparison between net dispersal distance of those owls that survived the autumn phase of transient dispersal ($\bar{x} = 32.0$ km, SD = 13.9, $n = 14$) and those that did not ($\bar{x} = 34.8$ km, SD = 21.3, $n = 18$).

DISCUSSION

Juvenile spotted owls selected closed-canopy forests over open-canopy forests during both the transient and colonization phases of natal dispersal. Our observation of a selection for older closed-canopy forests by spotted owls during natal dispersal confirms similar preliminary results in a dispersal study conducted in California (Gutiérrez et al., unpubl. data), and thus strengthens the association between owls and older forests previously established (Forsman et al. 1984, Carey et al. 1990, Ripple et al. 1991). Although owls selected closed-canopy forests over open-

Fig. 4.   Mean percent use and availability, based on the extent of fragmentation, during colonization dispersal of juvenile spotted owls (*n* = 17), western Oregon, 1982–85. Error bars represent standard error.

canopy forests during both natal dispersal periods, the magnitude of that habitat selection was not equal between the periods. Owls demonstrated a more distinct selection between closed- and open-canopy forests and relatively greater selection for older forests during colonization as compared to transience. Preliminary results from a study in Washington (Allen and Brewer 1985) also indicated a lack of strong habitat selection by juvenile spotted owls during dispersal.

The selection for older forests during the colonization phase of dispersal, accompanied by large individual selection variability (Fig. 2), further indicates the need for more intensive habitat use studies within these forests. Because spotted owls remain in the colonization phase of dispersal until they breed at 2–3 years of age (Thomas et al. 1990) and, in general, subadult spotted owls have a lower estimated fecundity than adults (Burnham et al. 1994), an increased understanding of habitat selection within older forests would help determine if age-specific selection strategies occur and how important they are to survival. Newton (1991*b*) proposed that the probability of breeding by sparrowhawks (*Accipter nisus*) is influenced by an interaction between foraging efficiency and habitat quality (based on food supply). Newton and Marquiss (1991) reported that breeding attempts by younger (often less efficient foragers) sparrowhawks were indeed dependent on the availability of "high quality" habitat. Thus, future habitat use studies of spotted owls within older forests should include concurrent estimates of age-specific survival and reproduction to provide an understanding of the processes which govern species-
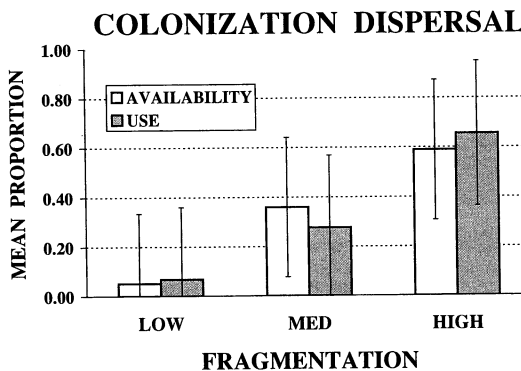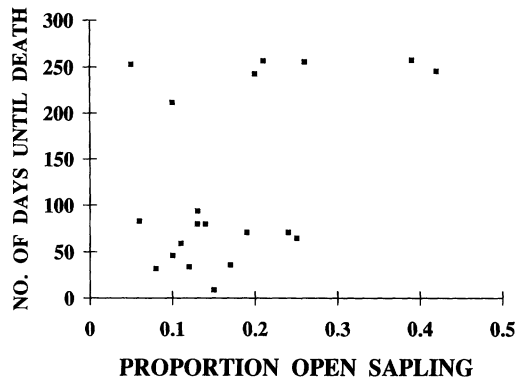
Fig. 6. Mean percent open sapling used during transient dispersal (*n* = 20) of juvenile spotted owls in western Oregon, 1982–85, compared to the number of days they survived after the initiation of transient dispersal.
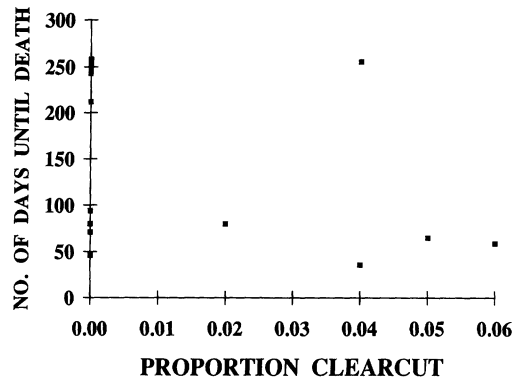

Fig. 7. Mean percent clearcut used during colonization dispersal (*n* = 16) of juvenile spotted owls in western Oregon, 1982–85, compared to the number of days they survived after the initiation of transient dispersal.

habitat relations (Van Horne 1986, Murphy and Noon 1991).

Dispersing juvenile owls selected equally between less fragmented forests and more fragmented forests. Although quantifying forest fragmentation is difficult (Morrison et al. 1992), indirect evidence of how fragmentation could affect dispersal comes from our observation of a negative relation between dispersal distance and the percentage of clearcut used during transience. This result suggests that the presence of clearcuts may decrease the propensity for continued transient dispersal, i.e., clearcuts may represent a barrier. Similarly, several juveniles encountering potential barriers (e.g., cities or major agricultural areas) terminated transience and settled next to the barrier (Miller 1989). Hence, although fragmentation will require owls to disperse greater distances to locate older forest patches, owls that confront clearcuts while dispersing in fragmented forests may actually reduce their dispersal distance. Dispersal distance has been a major factor in the design of conservation strategies for the spotted owl and has been one of the key components considered for spacing of both Habitat Conservation Areas outlined in the Interagency Scientific Committee Report (Thomas et al. 1990), the Designated Conservation Areas outlined in the final draft Northern Spotted Owl Recovery Plan (U.S. Dep. Inter. 1992), and Late Successional Reserves as developed by the Forest Ecosystem Management Assessment Team (FEMAT; U.S. Dep. Agric. et al. 1993).

The probability of mortality of dispersing juvenile owls was affected by their habitat selection during dispersal, as the likelihood of death decreased with increased use of open sapling stands during transience and increased with use of clearcuts during colonization. How an increased association with open sapling stands during transience would decrease mortality is difficult to interpret. Such stands were ranked lowest (along with clearcuts) in our habitat selection analyses, and Forsman et al. (1984) reported a similar low use of those habitat types for adult spotted owls. Prey availability probably is a critical factor during dispersal, because many dispersing spotted owls die from starvation (Miller 1989, Gutiérrez et al., unpubl. data); food supply is also critical to the survival of Tengmalm's owls (*Aegolius funereus*) during natal dispersal (Korpimäki and Lagerström 1988). Thus, a possible explanation for the decreased mortality associated with open sapling stands is that they could provide a relatively high source of prey compared to other habitats. The dusky-footed woodrat (*Neotoma fuscipes*) is the dominant prey species for spotted owls in the mesic forests of southern Oregon (Forsman et al. 1984), and attained highest densities in "sapling/brushy poletimber stands" (similar in vegetation structure to our open sapling stands) in northwest California (Sakai and Noon 1993). Sakai and Noon (1993) suggested that because dusky-footed woodrats will disperse from open sapling stands into adjacent older forest stands commonly used by owls, that such sapling stands would be beneficial to owls if owls were limited by prey availability. We suggest that dispersal may be limited by prey availability, because the majority of deaths during dispersal are from

starvation (Miller 1989). Thus, sapling stands may benefit owls by providing a source of prey that decreases mortality. We recognize that the northern flying squirrel (*Glaucomys sabrinus*), a species not associated with open sapling stands, replaces the woodrat as the dominant prey item in the central Cascades and Coast ranges of western Oregon. Hence, our interpretation does not suffice for those parts of our study area where flying squirrels are the predominant prey.

An increased probability of mortality with an increased use of clearcuts during colonization supports the contention that such open areas decrease successful dispersal. As only 1% of the habitat use by roosting owls was in clearcuts, this result is striking; yet, should be considered tentative given the small sample size. In a preliminary report, juvenile spotted owls in California that entered unsuitable habitat, including clearcuts, also appeared to suffer higher mortality (Gutiérrez et al. 1985). Two factors may contribute to increased mortality in clearcuts: a greater vulnerability to avian predation by great horned owls (*Bubo virginianus*) and northern goshawks (*Accipiter gentilis*) as suggested by Dawson et al. (1987); and decreased foraging activity, resulting in starvation, following the termination of dispersal at an abrupt habitat edge (Miller 1989; E. Forsman, U. S. For. Serv., pers. commun.).

Obtaining information on dispersal dynamics useful in developing management and conservation strategies remains a fundamental challenge. Defining habitat availability during dispersal was essential to our research, and we recognize our conclusions depend upon that definition (Johnson 1980). Specifically, Johnson (1980) discussed the concept of a hierarchy of habitat selection where the order of selection is dependent on previous selection processes, e.g., selection of (1) geographical range, (2) home range, and (3) habitat components within the home range. Spotted owls select habitats at all 3 orders during dispersal, thus confounding the concept of availability. We defined habitat availability during dispersal from the estimated dispersal paths of individual owls, as opposed, for example, to all habitats available in a larger area surrounding the nest site (natal area). Hence our inferences are based on the assumption that owls already displayed some level of selection. Our estimate of older forests as the most abundant available habitat demonstrates such prior selection by dispersing juvenile owls, because

these forests do not comprise the most abundant habitat in the overall study areas.

MANAGEMENT IMPLICATIONS

Natural resource managers require an understanding of the effect of habitat-management activities on the viability of wildlife populations (Marcot 1986). Our research indicates that spotted owls selected older closed-canopy forests during natal dispersal, reinforcing the strong association between this species and such forests. Thus, the question of how the continued loss and fragmentation of older closed-canopy forests will affect the viability of owl populations depends, in part, on the distribution of remaining forests relative to the owls' ability to locate them (McLellan et al. 1986, Pulliam and Danielson 1991). Morrison et al. (1992:87) recommended that patches of rare habitat be accessible to species that demonstrate strong habitat selection, such as the spotted owl. Maintaining some older forest in the matrix surrounding the patches occupied by breeding adults will provide colonization areas for subadults during the years before their recruitment into the breeding population, and potential travel corridors for both juvenile and displaced adult owls during transient dispersal. Selection of older closed-canopy forests during dispersal supports the concept of maintaining adequate dispersal habitat (through a variety of means) among designated reserve areas as described in the Interagency Scientific Report (Thomas et al. 1990), final draft Northern Spotted Owl Recovery Plan (U.S. Dep. Inter. 1992), and the FEMAT Report (U.S. Dep. Agric. et al. 1993). Alternative management strategies such as the draft Preservation Plan for the Northern Spotted Owl (Lujan et al. 1992) would not be supported by our results because adequate dispersal conditions would not be maintained over a large portion of the species' range and important connections between physiographic provinces would be lost. Because our results indicate that dispersal distances decline as juvenile owls disperse through clearcuts, and use of clearcuts may increase their mortality, we recommend a reduction in the number of clearcuts to increase successful dispersal. Such a reduction in clearcuts not only should facilitate more successful transient dispersal, but provide for some level of older forest being maintained throughout the matrix for colonization by young owls. Additional information on the dynamics of owl dispersal, particularly habitat-specific

survival rates, is needed to develop better management and conservation strategies.

LITERATURE CITED

ALLEN, H., AND L. W. BREWER. 1985. A review of current northern spotted owl (Strix occidentalis caurina) research in Washington State. Pages 55–57 in R. J. Gutiérrez and A. B. Carey, tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. U.S. For. Serv. Gen. Tech. Rep. PNW-185.

ALLDREDGE, J. R., AND J. T. RATTI. 1986. Comparison of some statistical techniques for analysis of resource selection. J. Wildl. Manage. 50:157–165.

———, AND ———. 1992. Further comparison of some statistical techniques for analysis of resource selection. J. Wildl. Manage. 56:1–9.

BURNHAM, K. P., D. R. ANDERSON, AND G. G. WHITE. 1994. Estimation of vital rates of the northern spotted owl. Appendix J. Pages 1–26 in Final Supplemental Environmental Impact Statement on management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. U.S. Dep. Inter. Vol. 2. Portland, Oreg.

CAREY, A. B., J. A. REID, AND S. P. HORTON. 1990. Spotted owl home range and habitat use in southern Oregon coast ranges. J. Wildl. Manage. 54:11–17.

CONOVER, W. J. 1980. Practical nonparametric statistics. Second ed. John Wiley and Sons, New York, N.Y. 493pp.

COX, D. R. 1972. Regression models and life tables. J. R. Stat. Soc. Ser. B 34:187–220.

DAWSON, W. R., J. D. LIGON, J. R. MURPHY, J. P. MYERS, D. SIMBERLOFF, AND J. VERNER. 1987. Report of the scientific advisory panel on the spotted owl. Condor 89:205–229.

DAY, R. W., AND G. P. QUINN. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecol. Monogr. 59:433–463.

DOAK, D. 1989. Spotted owls and old growth logging in the Pacific Northwest. Conserv. Biol. 3:389–396.

FORSMAN, E. D. 1983. Methods and materials for locating and studying spotted owls. U.S. For. Serv. Gen. Tech. Rep. PNW-162. 8pp.

———, E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the spotted owl in Oregon. Wildl. Monogr. 87. 64pp.

FRANKLIN, J. F., AND C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S. For. Serv. Gen. Tech. Rep. PNW-8. 417pp.

GREENWOOD, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. Anim. Behav. 28:1140–1162.

GUTIÉRREZ, R. J., A. B. FRANKLIN, W. LaHAYE, V. J. MERETSKY, AND J. P. WARD. 1985. Juvenile spotted owl dispersal in northwestern California: preliminary results. Pages 60–65 in R. J. Gutiérrez and A. B. Carey, tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. U.S. For. Serv. Gen. Tech. Rep. PNW-185.

HALL, F. C., L. W. BREWER, J. F. FRANKLIN, AND R. L. WERNER. 1985. Plant communities and stand conditions. Pages 17–31 in E. R. Brown, tech. ed. Management of wildlife and fish habitats in forests of western Oregon and Washington. U.S. For. Serv. Publ. R6-F and WL-192.

HARRISON, R. L. 1992. Toward a theory of inter-refuge corridor design. Conserv. Biol. 6:293–295.

HARRISON, S., A. STAHL, AND D. DOAK. 1993. Spatial models and spotted owls: exploring some biological issues behind recent events. Conserv. Biol. 4:950–953.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

———. 1994. Population analysis. Pages 419–444 in T. A. Bookhout, ed. Research and management techniques for wildlife and habitats. Fifth ed. The Wildl. Soc., Bethesda, Md.

JOHNSON, M. L., AND M. S. GAINES. 1985. Selective basis for emigration of the prairie vole, Microtus ochrogaster: open field experiment. J. Anim. Ecol. 54:399–410.

KAREIVA, P. 1990. Population dynamics in spatially complex environments: theory and data. Philos. Trans. R. Soc. London, U.K. 330:175–190.

KORPIMÄKI, E., AND M. LAGERSTRÖM. 1988. Survival and natal dispersal of fledglings of Tengmalm's owl in relation to fluctuating food conditions and hatching date. J. Anim. Ecol. 57:433–441.

LAMBERSON, R. H., R. MCKELVEY, B. R. NOON, AND C. VOSS. 1992. A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. Conserv. Biol. 4:505–512.

———, B. R. NOON, C. VOSS, AND K. S. MCKELVEY. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the northern spotted owl. Conserv. Biol. 8:185–195.

LANDE, R. 1991. Population dynamics and extinction in heterogeneous environments: the northern spotted owl. Pages 566–580 in C. M. Perrins, J. D. Lebreton, and G. J. M. Hirons, eds. Bird population studies. Oxford Univ. Press, Oxford, U.K.

LUJAN, M., JR., J. H. BEUTER, E. CASSIDY, J. M. HAYDEN, D. C. O'NEAL, AND J. E. SCHROTE. 1992. Preservation plan for the northern spotted owl—draft. U.S. Dep. Inter., Washington, D.C. 44pp.

MARCOT, B. G. 1986. Biometric approaches to modeling—the manager's viewpoint. Pages 203–204 in J. Verner, M. L. Morrison, and C. J. Ralph, eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison.

MCLELLAN, C. H., A. P. DOBSON, D. S. WILCOVE, AND J. F. LYNCH. 1986. Effects of forest fragmentation on new- and old-world bird communities: empirical observations and theoretical implications. Pages 305–313 in J. Verner, M. L. Morrison, and C. J. Ralph, eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison.

MILLER, G. S. 1989. Dispersal of juvenile northern

spotted owls in western Oregon. M.S. Thesis, Oregon State Univ., Corvallis. 139pp.

――――, AND E. C. MESLOW. 1985. Dispersal data for juvenile spotted owls: the problem of small sample size. Pages 69–73 *in* R. J. Gutiérrez and A. B. Carey, tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. U.S. For. Serv. Gen. Tech. Rep. PNW-185.

MORRISON, M. L., B. G. MARCOT, AND R. W. MANNAN, EDITORS. 1992. Wildlife-habitat relationships: concepts and applications. Univ. Wisconsin Press, Madison. 343pp.

MUNGER, T. T. 1930. Ecological aspects of the transition from old forests to new. Science 72:327–332.

MURPHY, D. D., AND B. R. NOON. 1991. Coping with uncertainty in wildlife biology. J. Wildl. Manage. 55:773–782.

NEWTON, I. 1991*a*. Concluding remarks. Pages 637–654 *in* C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, eds. Bird population studies. Oxford Univ. Press, Oxford, U.K.

――――. 1991*b*. Habitat variation and population regulation in sparrowhawks. Ibis 133 Suppl. 1:76–88.

――――, AND M. MARQUISS. 1991. Removal experiments and the limitation of breeding density in sparrowhawks. J. Anim. Ecol. 60:535–544.

NOON, B. R., AND C. M. BILES. 1990. Mathematical demography of spotted owls in the Pacific Northwest. J. Wildl. Manage. 54:18–27.

PULLIAM, H. R., AND B. J. DANIELSON. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. Am. Nat. 137:S50–S66.

――――, J. B. DUNNING, JR., AND J. LIU. 1992. Population dynamics in complex landscapes: a case study. Ecol. Appl. 2:165–177.

RIPPLE, W. J., D. H. JOHNSON, K. T. HERSHEY, AND E. C. MESLOW. 1991. Old-growth and mature forests near spotted owl nests in western Oregon. J. Wildl. Manage. 55:316–318.

ROLSTAD, J. 1991. Consequences of forest fragmentation for the dynamics of bird populations: conceptual issues and the evidence. Biol. J. Linnean Soc. 42:149–163.

SAKAI, H. F., AND B. R. NOON. 1993. Dusky-footed woodrat abundance in different-aged forests in northwestern California. J. Wildl. Manage. 57:373–382.

SMALL, R. J., J. C. HOLZWART, AND D. H. RUSCH. 1993. Are ruffed grouse more vulnerable to mortality during dispersal? Ecology 74:2020–2026.

SOULÉ, M. E., AND K. A. KOHM. 1989. Research priorities for conservation biology. VI. Fragmentation. Island Press, Washington D.C. 97pp.

TAYLOR, A. D. 1990. Metapopulations, dispersal, and predator-prey dynamics: an overview. Ecology 71:429–433.

TEMPLE, S. A. 1989. The role of dispersal in the maintenance of bird populations in a fragmented landscape. Acta Congr. Int. Ornithol. 20:2298–2305.

THOMAS, D. L., AND E. J. TAYLOR. 1990. Study designs and tests for comparing resource use and availability. J. Wildl. Manage. 54:322–330.

THOMAS, J. W., E. D. FORSMAN, J. B. LINT, E. C. MESLOW, B. R. NOON, AND J. VERNER. 1990. A conservation strategy for the northern spotted owl. A report by the Interagency Scientific Committee to address the conservation of the northern spotted owl. U.S. For. Serv., Portland, Oreg. 427pp.

U. S. DEPARTMENT OF AGRICULTURE, U. S. DEPARTMENT OF THE INTERIOR, U. S. DEPARTMENT OF COMMERCE, AND THE ENVIRONMENTAL PROTECTION AGENCY. 1993. Forest ecosystem management: ecological, economic, and social assessment. U.S. For. Serv., U.S. Fish and Wildl. Serv., Natl. Mar. Fish. Serv., Natl. Park Serv., Bur. Land Manage., and Environ. Prot. Agency. 1007pp.

U.S. DEPARTMENT OF THE INTERIOR. 1992. Recovery plan for the northern spotted owl—final draft. U.S. Dep. Inter., Portland, Oreg. Vol(s). 1 and 2. 812pp.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47:893–901.

――――. 1986. When habitats fail as predictors—the researcher's viewpoint. Pages 257–258 *in* J. Verner, M. L. Morrison, and C. J. Ralph, eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison.

WEINS, J. A. 1990. Habitat fragmentation and wildlife populations: the importance of autecology, time, and landscape structure. Trans. Int. Congr. Game Biol. 19:381–391.